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EFFECT OF LOW TEMPERATURE ON THE HATCHING OF GIPSY-MOTH EGGS.

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CONTENTS.

	Page.		Page.
Introduction	1	Temperature resistance	5
Preliminary discussion	1	Summer survey of hatching	5
First investigations	2	Weather	6
Method of handling all egg clusters used in experiments	3	Results obtained from experiments	6
Monthly collections	3	Results of summer survey of hatching	9
Month's exposure	4	Effectiveness of nonhatch	11
Natural protection	4	Effects of cold on parasites	12
Artificial protection	4	Conclusions	13
Exposures of clusters to one severe drop in temperature	5		

INTRODUCTION.

Extensive study of the gipsy moth (*Porthetria dispar* L.), made in connection with the introduction, establishment, and dispersion of its parasites, has shown that in New England there are agencies of natural control responsible for a considerable mortality among the various stages.

One of these natural-control agencies, which in many cases is the most valuable, acts upon the eggs and causes a failure to hatch. This phenomenon has been termed nonhatch. The results of several years' study are presented in this bulletin.

PRELIMINARY DISCUSSION.

The failure of gipsy-moth eggs to hatch has been common enough to attract attention during the last few years only. As will be shown later, very low temperatures are responsible for this killing, and until about 10 years ago the moth had not spread into territory having such low temperatures regularly. It is probable that even in the older infested area there were isolated pockets which, owing to topography, attained temperatures low enough to kill. Likewise it is probable that a careful examination of some of the egg clusters which

apparently hatched well would have shown considerable injury. Such points, however, would only have been brought out by an intensive study in the woodland, such as was started later. A few records of entire clusters failing to hatch were made in 1907, notably in North Saugus, Mass., in woodland near the building then used as a laboratory for the parasite investigations.

During the winter of 1911–12 plans were perfected for an extensive and intensive study of the gipsy moth under natural conditions. These plans called for the selection of a considerable number of small areas, well proportioned as to type of tree growth and so placed as to be representative of the entire infested area. The areas designated as "observation points" were to be followed closely during the entire year, with careful notes on hatching of the gipsy-moth eggs, feeding of the larvæ and the injury done by them, the increase or decrease of the infestation from year to year, and many other phases of the subject. As the entire problem was built around the degree of infestation, it became necessary to have an accurate knowledge of the number of egg clusters present in each "point." Therefore, each fall or winter a careful count was made, and it was this counting which brought forcibly to the attention of those engaged in experimental work that some agency was playing a considerable part in the control of the moth by killing the eggs.

The nonhatch problem did not receive extensive experimental attention until the fall of 1915, when preliminary work was started.

FIRST INVESTIGATIONS.

At first considerable time was devoted to the study of the nonhatch eggs themselves. Such individual eggs collected a few months after the end of the normal hatching season, as well as those 1 or 2 years old, were all light gray in color. Careful dissection showed that this appearance was due to a complete, closely woven mat of fungus mycelium which was pressed closely against the inside of the shell and entirely surrounded the dead embryo. The presence of this organism in all the nonhatch eggs made it appear that there might be some connection between it and the death of the embryo. Cultural studies were made, and a considerable number of infection experiments were carried on, which, however, failed to give more than vague evidence that the fungus was ever more than a saprophyte. It is possible that this organism, belonging in the large and rather indefinite genus Fusarium, is, under conditions particularly favorable to itself, a true parasite. However, extensive dissections and cultures made of nonhatched eggs as soon as it was shown that they were not going to hatch have yielded no positive evidence of its being parasitic.

The first real study of nonhatch in the field was begun in the fall of 1916.[1] Previous to this a series of egg-cluster collections had been made, beginning in August, 1915, and continuing at monthly intervals until just before normal hatching time in the spring of 1916. Six sets of these collections were made, five being obtained at chronic

[1] The writer wishes to express his appreciation of the able assistance given him by Mr. H. I. Winchester, who helped with the experiments for almost the entire time they were conducted. During the time the writer was in the Army, Mr. Winchester conducted all the experiments, and to him belongs the credit for planning and making the summer observations on hatching.

nonhatch points—that is, points at which considerable nonhatch had been noted each year since the start of the "observation-point" investigations. The sixth set, collected as controls, was obtained from a point which had not shown nonhatch. All the clusters thus obtained were kept in a cool place at the laboratory from the time of collection until just before normal hatching time in the spring. Each cluster was then placed in a glass tube and allowed to hatch normally. All larvæ thus produced were counted, and later, when hatching had ceased, the remains of the clusters were rubbed over a cheesecloth sifter to separate the unhatched eggs from the hair with which the egg cluster is made.

As soon as the records from the six sets of collections could be studied it was seen that there appeared to be some connection between nonhatch and cold weather, for clusters obtained from the five points before our normally cold months hatched almost perfectly, while those obtained after the cold season began failed to produce larvæ.

This suggestion opened up a new line for investigation, and accordingly three sets of weather instruments, each consisting of a recording thermometer and a recording hygrometer, were procured and placed in small instrument houses. As the instruments required considerable attention the three houses were placed at points in the towns of Westford, Acton, and Dover, Mass., two being chronic nonhatch and the third no nonhatch, not very many miles from the Melrose Highlands Laboratory.

The instruments were started September 1, about the end of the laying season, and were run continuously until about May 1, the normal hatching time. They were tested for accuracy at frequent intervals to insure true records, a discussion of which will be given later.

METHOD OF HANDLING ALL EGG CLUSTERS USED IN EXPERIMENTS.

Egg clusters when brought in to the laboratory were placed where they would be kept cool but not exposed to severe weather. Just before normal hatching time, which is about May 1 at Melrose Highlands, each cluster was placed in a glass tube large enough to contain it unbroken. This tube was closed with a cotton plug. As soon as hatching was well advanced, the larvæ were removed from the tubes and counted. At the end of the hatching season, the remains of each cluster were rubbed over a cheesecloth sifter, made by stretching fine-meshed cheesecloth over a frame, to separate the unhatched eggs from the mass of hair with which all clusters are made. These unhatched eggs were then examined microscopically and divided into infertile and nonhatch, the records of each cluster being kept separately.

MONTHLY COLLECTIONS.

Some of the clusters collected during the season of 1915–16 proved to be old nonhatch. During the winter, after the new clusters have become weathered, it is difficult to distinguish between old and new. To make certain that only new clusters would be collected, a sufficient number of these were marked with lumber crayon at the end of each laying season at the same six points used for the collections

of 1915–16. Ten clusters were collected at each point on the first of each month, beginning in September and ending in April. Subsequently they were handled exactly as described.

As the sets of weather instruments were located at three of the collection points, the records obtained from these are the most valuable. The other three, however, were kept as collection points for purposes of comparison.

MONTH'S EXPOSURE.

As controls on the naturally produced egg clusters obtained in "monthly collections," a series of experiments were conducted with clusters produced at the laboratory. To obtain these, vigorous males and females were mated in a small cage, and later the females were confined in small tin boxes, where they deposited their eggs upon pieces of thin wood.

Ten such clusters were tacked to trees at each point where there were weather instruments and allowed to remain in the open just one month. The first set was out from September 1 to October 1, the second from October 1 to November 1, and so on. The last set placed out April 1 was brought in just before hatching time. After exposure the clusters were handled as in all the other experiments.

NATURAL PROTECTION.

Notes taken in connection with the "observation-point" investigations showed that in certain localities there was considerable difference in hatching on different parts of the trees. Clusters found under roots or in cavities close to the ground, as well as those fully exposed close to the ground, appeared to hatch completely, while those higher up failed to do so.

Investigation at a number of chronic nonhatch points proved that in general it would be rather difficult to find enough clusters naturally deposited where they were wanted. Therefore, at each of the six points from which monthly collections were obtained 100 new clusters were cut from the trees and tacked back in the following positions:

Twenty-five clusters were tacked under roots or in cavities close to the ground. Usually these were covered with leaves.

Twenty-five at the base of a tree close to the ground but entirely in the open.

Twenty-five on the trunk well up from the ground, usually about 5 feet.

The remaining 25 were brought in to serve as controls.

Collection of these clusters was made just before hatching time each spring.

ARTIFICIAL PROTECTION.

Originally these experiments were planned when the fungus found in the nonhatch eggs was looked upon as a possible cause. Various means were tried of protecting the clusters against infection, but most of these were abandoned when the true nature of the fungus became apparent.

Two experiments in artificial protection were continued. The first, by means of a wire cage suspended between trees, sought to protect the clusters contained therein from any influence the tree

might have and at the same time expose them fully to all actions of the elements. The second was an endeavor to protect the clusters from wind and rain or snow, but to expose them to fluctuations in temperature and atmospheric moisture. This was accomplished by placing them in open inverted preserving jars and holding them up near the bottom with wire screen. The jars were wired to tree trunks.

Both types of artificial protection were performed with laboratory-bred clusters and were put out at a considerable number of chronic nonhatch points. The clusters were brought to the laboratory in the spring and handled like all the other experimental clusters.

EXPOSURES OF CLUSTERS TO ONE SEVERE DROP IN TEMPERATURE.

After results from some of the other experiments had pointed rather conclusively to low temperatures as the cause of nonhatch, it was desirable to gain more information on the degree of cold and the extent of exposure necessary to kill.

It was planned to expose sets of clusters to a single severe drop, beginning with —15° F., apparently the temperature at which the first killing took place. It was hoped that a complete chain would be obtained from —15° downward as far as the thermometer goes at the points where the weather instruments were placed. This was not found to be possible, as one could not foresee the temperature fluctuations. A certain number of such sets of clusters, however, were exposed.

The sets of laboratory-bred clusters were placed near the weather instruments and allowed to remain until they had been exposed to a single drop of at least —15°. They were then brought in and handled like other clusters.

TEMPERATURE RESISTANCE.

Sets of 10 laboratory-bred clusters were exposed during the winter in small wire cages along the line marking the northern limits of the gipsy-moth area. These were placed in towns from which the Weather Bureau office at Boston obtains records, so that a close record of the cold might be available, for it was desired to note the effect of as extreme cold as possible.

These remained out all winter until just before hatching time, when they were brought to the laboratory.

SUMMER SURVEY OF HATCHING.

Each summer for three years, after the hatching season was over, an extensive series of observations on hatch was made in the field. Practically the entire area of infestation was gone over from the most southern limits to the most northern, and a very large number of observations were made. Fortunately it was possible to make these observations after two very cold winters and one very mild one, the latter coming between the two cold ones.

WEATHER.

The instruments located at the three points gave records of temperature and relative humidity. As soon as these records for the

tained from the last two. All of these were conducted at chronic nonhatch points.

Those clusters placed in the wire cages were entirely removed from any influence the trees might have upon them and were fully exposed to all actions of the elements. Very little information was obtained from this series beyond the fact that clusters reacted the same way no matter how they were placed.

During the cold years all of these clusters were killed, as were those naturally on the trees. After the mild winter they all hatched completely.

Those clusters in the inverted jars received a considerable amount of protection, as they were in no way affected by storms. Low temperature could act upon them freely and to a certain extent the atmospheric moisture could do so, for the jars were open at the bottom, allowing air to ascend into them when it became warm. No rain or snow could reach them, however, and as a result they remained perfectly dry during the entire winter, as was proved by numerous observations. They were therefore not frozen or covered with ice, as were many of the clusters in the open.

These clusters were only exposed to temperature and atmospheric moisture. It has been shown already that humidity can play very little, if any, part in killing the eggs; therefore it may be considered that if these eggs were killed temperature must have been responsible. To corroborate this conclusion all eggs exposed in this manner failed to hatch after the cold winters, but hatched perfectly after the mild one.

Experiments in natural protection were suggested by notes taken in connection with the "observation point" investigations, as has already been noted. It was found that those placed close to the ground at nonhatch points, whether in cavities, under roots, or in the open, hatched completely, while those high up were killed. At first sight snow appeared to be the protecting factor; and this supposition was borne out later by actual observation, though it was some time before all variations could be reconciled with this theory. To afford protection the snow had to cover the clusters during every severe cold spell, which it did not do because of the countless variations in its depth, and it was only after a long series of observations in the woods that a true appreciation of the variableness of this factor became apparent. Depth even immediately after the cessation of a storm varied enormously, particularly if the snow was light, for every breath of air induced drifting. Many times also the eddying of the wind around the tree trunks left the snow piled against one side and blown away from the other. The resulting depression served to expose some clusters while others remained covered, a fact which explains why clusters close to the ground were killed and those much higher hatched.

A close following of the snow history of a section during the winter showed great fluctuations in depth, when measured on the trunk of a tree small enough to be unaffected by the wind eddies mentioned above. At the end of a storm the snow would be piled to a certain height on the tree; then gradually settling would take place, until after the lapse of a few days there would be several inches difference

between the new level and the old. A new storm might then come and cause the level to rise again. So it went during the entire winter, and clusters on the border line of snow protection were alternately exposed and protected. Observation made on some such clusters proved conclusively that the snow is the medium of protection.

There remains only one series of experiments to be discussed, namely, temperature resistance, which was conducted for two years only. As it developed, the first year selected for this type was, very opportunely, the mild winter 1918–19. The only killing of eggs for that year that was recorded in our experiments developed in some of these sets of clusters exposed at the northernmost limits of the gipsy-moth area, in the only towns from which records anywhere near —20° F. were taken. After the next winter, as was to be expected, none of the clusters in this series hatched.

RESULTS OF SUMMER SURVEY OF HATCHING.

A few observations made in the field after the end of the hatching season which followed the extremely cold winter of 1917–18 disclosed the fact that there was an unusual amount of nonhatch. This gave a very good opportunity for a careful study under natural conditions. Accordingly, extensive plans were made to extend observations over as large a portion of the gipsy-moth area as possible. Results obtained from experiments had pointed strongly toward low temperature as the causative factor of nonhatch. To a certain extent, however, the experiments had an element of artificiality, and it was desired to obtain as much information as possible under purely natural conditions.

The plans called for observations on hatch of egg clusters on trees, undergrowth, stumps, débris on the ground, boulders, stone walls, and other objects. Many factors were taken into consideration, such as nearness to the ocean and bodies of fresh water, height of land, degree of exposure to prevailing winds, favorability or unfavorability of food plants and the abundance or scarcity of these, the degree of gipsy-moth infestation, and any other points which might present themselves. These observations were taken during the three summers 1918, 1919, and 1920.

The observations taken in the summer of 1918 disclosed a complete nonhatch of all clusters above the snow-protection line in Maine and New Hampshire, with the exception of a section along the seacoast. This section showed only a partial hatch. All clusters found on the ground or on other objects close to the ground where they could be snow-protected hatched completely. Hatching above the snow-protection line in Massachusetts, with the exception of a coastal section which included all of Cape Cod, was poor with a considerable number of whole clusters killed, particularly in the northern and northeastern parts. Hatching of low clusters in all this area was uniformly good.

In Rhode Island and along the coast as far north as the Massachusetts-New Hampshire line the hatch was almost complete.

Apparently the modifying influence of the ocean overcame the severe cold at least enough to prevent the temperature from dropping to the killing point all along the coast of Rhode Island and Massa-

chusetts. The area over which this modifying effect protected the eggs was wide in Rhode Island and Massachusetts, but it gradually narrowed northward until at Portsmouth, N. H., the only modification was right on the coast, and even there some of the eggs were killed. Farther north the cold was too great to be overcome sufficiently to allow the egg clusters to hatch completely, and only a partial hatch was recorded.

The Weather Bureau records show that the foregoing hatch records are just what would be expected if low temperature was the cause of nonhatch.

Bodies of fresh water apparently had no influence on the hatch.

Elevation made no difference except in sections right on the border line of killing cold, that is, sections which as a whole had temperatures not quite low enough to kill. In these sections clusters in low areas were killed while those on the higher levels escaped, a difference caused by cold draining into the low land and settling there.

The object upon which the clusters were placed had no effect, as no matter what it was, if they were above snow protection in a locality which had severe cold, they were killed.

Considerable observation on the possible influence of the food plants failed to show any difference. Records taken in any locality were uniform no matter what species of tree the eggs were laid upon, and irrespective of the abundance or scarcity of favored food. Of course this latter factor had some bearing on the abundance of clusters, but it made no difference in the nonhatch.

At only one place, a location right on the coast in Rye, N. H., was it possible to make a direct comparison between egg clusters completely exposed to the prevailing winds and others well protected from them. In a little grove about a quarter of a mile from the sea, exposed on its ocean side to the full sweep of northeast storms, the clusters on the windward side had the hairy covering entirely weathered away, leaving the eggs uncovered. These did not hatch. On the other side of the same grove other clusters were found which had not been deprived of their hairy covering. These hatched almost perfectly.

Following the mild winter of 1918–19, the same localities were visited again. Every cluster found, no matter what its position on the tree or other object, hatched perfectly. In fact, there was not a single nonhatch cluster found during the progress of the summer survey; neither was there one reported by men engaged in other branches of the gipsy-moth investigations.

The winter of 1919–20 was a complete contrast to its predecessor but was almost exactly the same in temperature as that of 1917–18. There was a considerably greater fall of snow in some localities, which gave protection to a greater number of clusters. Observations after this winter gave the same results as those after the other cold one, except that in some places which had more snow than during the other cold winter a greater number of clusters had hatched.

All of the results of the summer survey observations, compared with records of temperature obtained by the Weather Bureau, serve to add conclusiveness to the fact that low temperature is the cause of nonhatch.

EFFECTIVENESS OF NONHATCH.

Nonhatch as an agency in the natural control of the gipsy moth reaches the maximum of its importance in those sections of the infested area which have, some time during each winter, cold severe enough to kill all eggs exposed to its action.

The principal protection from this killing cold is afforded by the snow; and the upper limit of this protection, measured from the ground, has been designated as the snow-protection line. It must not be supposed that this line has any definite limits, for the depth of snow is an extremely variable factor.

To determine the value of nonhatch as an agency in gipsy-moth control it is therefore necessary to determine the distribution of the egg clusters on the trees, the factors which influence this distribution, and the proportion placed above the snow protection line. Fortunately a considerable amount of information along these very lines has been obtained during the progress of the "observation point" investigations.

The count of egg clusters made at each "point" was divided into two sections. The dividing line was marked at 5 feet from the ground on the trunks of the trees. The count of clusters above this line was known as the high count, of those below as the low count. Such a division was necessary on account of the work involved, which made impossible the complete counting of an entire point at one time. Many times also snow would prevent a low count but would not prevent the high count being taken. Five feet was chosen as a convenient point well above the usual snowfall.

As the clusters were recorded with reference to their position above or below this 5-foot line, it will have to be the dividing line considered in studying the distribution of clusters on the trees. A depth of snow to the extent of 5 feet is almost unknown in most sections of the gipsy-moth area, so we may safely consider that all the exposed egg clusters above 5 feet will be killed if the temperature drops to —20° F. or lower. At the same time there will probably be a considerable number of clusters between the 5-foot level and the top of the snow during at least one period of severe cold, so that we are conservative in using the high count as a basis for figuring benefit derived from nonhatch.

A careful consideration of the egg-cluster records from the "point" notes, which were taken during seven consecutive years, shows that on the average 70 per cent of the clusters are laid above 5 feet. An average of nearly 900 individual counts showed 72 per cent.

The deposition of clusters is influenced largely by the ground conditions. If there is no underbrush and if débris, such as dead wood, bark, etc., is not present or if the ground is wet, most of the clusters will be well up on the trees. On the other hand, if débris is abundant, if there is much undergrowth, or if, as often happens in New England, there are stone walls running through the woods, a large proportion of the clusters will usually be found close to the ground.

It is not possible to say just what causes the differences, but the "point" notes show that they are as stated. In addition, the records

show that unless some change takes place, such as removing the débris or increasing it by brush from cutting, the proportion of those above and below the 5-foot line will remain approximately the same. Having determined 70 per cent as being the average proportion of egg clusters laid above 5 feet, we can see just how valuable as a means of control nonhatch may be where the cold is sufficiently severe to kill all unprotected clusters.

This particularly desirable state of affairs can not be looked for in a large part of the territory, for the temperature does not go low enough. The "point" notes show all variations between the above-mentioned percentage and no killing at all. Occasionally there is a mild winter with no low temperature and all eggs hatch the following spring.

As nonhatch is caused by a temperature of from —20° to —25° F. we can only expect to find it in territory subjected to such low degrees. Temperature records obtained from the 50 stations of the Weather Bureau which are located in the present area of infestation show that any prophecy as to just what would happen in any locality would be quite useless. If the law of averages may be considered in this case, killing cold will occur in a majority of years in all of Maine and New Hampshire except a narrow area along the coast. In Massachusetts such cold, at least as reported by the weather stations, is the exception, but there appears to be a greater tendency toward it in Worcester County and the northern part of Middlesex County. The remainder of the infested area, with the exception of the northern part of Windham County in Connecticut from which extreme low temperatures are occasionally reported, apparently escapes cold severe enough to kill the eggs.

These general conclusions, based as they are upon Weather Bureau records, apply to the sections as a whole. Local conditions, however, vary to such an extent that we may find nonhatch in restricted areas in sections from which temperature records would apparently exclude it. "Observation point" investigations prove this to be particularly true of northern and central Massachusetts.

It is possible that nonhatch is responsible for the slow increase of the gipsy moth in many localities where food conditions would seem to point to just the reverse.

EFFECTS OF COLD ON PARASITES.

There is reason to suppose that a drop in temperature low enough to kill the eggs will have some effect upon the imported parasites, particularly those which attack the eggs themselves. Two egg parasites, namely, *Anastatus bifasciatus* Fonsc. and *Schedius kuvanae* How., have become well established in New England. The former passes the winter as a full-grown larva within the egg of the host. No collections of eggs parasitized by *Anastatus bifasciatus* have been made after extremely cold weather for the specific purpose of determining the effect of cold upon this parasite. It was noted, however, that there was a large percentage of dead parasites in a bulk collection of eggs obtained after the cold winter of 1917–18. The locality from which this collection came has been used for a number of years as a source of material for new colonies, and eggs

collected there had each year shown a high percentage of parasitism. After the above-mentioned cold winter the parasitism was of decidedly lower percentage, but two years later it had about reached its former high point.

In the long run it is doubtful if the cold would have any very serious effect upon the general abundance of *Anastatus bifasciatus*. Even though all the parasites as well as all the eggs above the snow protection line were killed, the proportion of parasites to eggs would be the same in those egg clusters protected by the snow, for there is very little difference in percentage of parasitism between eggs near the ground and those above 5 feet. Therefore, there would be the same proportion of adult parasites to attack the eggs the next summer as if all parasites and all eggs came through the winter safely.

As the result of particularly adverse conditions a decrease in parasitism by *Anastatus bifasciatus*, such as was evidenced at the stock colony, may occur for a few years, but no doubt there is a gradual recovery.

Schedius kuvanae has received some rather severe setbacks from cold winters. It hibernates as an adult, principally in leaves and rubbish on the ground, and in such position it would be well protected from the cold if there was plenty of snow during each period of extremely low temperature. Apparently such protection has not been present in a number of cases, for there are records of colonies from which recovery of parasites was difficult after a severely cold winter.

Some of the other imported parasites may be killed by low temperature, but very little information has been obtained to confirm this idea.

Further investigations may throw more light upon the relationship of low temperature to parasite mortality.

CONCLUSIONS.

The failure of gipsy-moth egg clusters to hatch is caused by low temperature.

An exposure of between —20° and —25° F. is necessary to kill entire clusters, though some eggs in each cluster may be killed by an exposure to —15°. No eggs will survive an exposure to lower than —25°.

When the temperature is low enough, an average of 70 per cent of the clusters may be killed, but this desirable condition develops only in the northern part of the infested area and only during certain years.

Snow will protect the egg clusters from the effects of the cold if it covers them; therefore, the greater the depth of snow the larger the number of clusters that will hatch the following spring.

The benefit derived from nonhatch may vary after a cold winter from 70 per cent of the clusters killed in the northern part of the area to no injury to the eggs in the southern section.

Maine and New Hampshire receive the greatest benefit from nonhatch. Central and northern Massachusetts also derive considerable benefit particularly in restricted localities. Connecticut, Rhode

Island, the southern and eastern parts of Massachusetts, and the coastal section of New Hampshire derive very little, if any, benefit, for even after the coldest winters nearly all eggs hatch.

Nonhatch is of a periodic nature, as occasionally New England is visited by a mild winter, after which practically all eggs hatch.

The benefit derived from nonhatch is offset to some extent by the injury cold weather works upon the parasites of the moth.

As temperature is entirely uncontrollable, there is no way that man may direct its action against the gipsy moth.

Finally, too much reliance must not be placed on nonhatch as a means of control, for it occurs only after the egg clusters have been exposed to the proper degree of cold.

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